

## **Constraining pollen-based estimates of forest cover in the Amazon: A simulation approach**

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### **Abstract**

Pollen Dispersal and Deposition (PDD) modelling has been instrumental in reconstructing historical vegetation in temperate regions but its application has been limited in the tropics where there is greatest uncertainty in past land cover change. Here, we apply PDD modelling to Amazonian savanna and forested ecosystems. Empirical pollen data from lakes situated in Southwestern Amazonia were used to calibrate the PDD model for a two-component landscape of forest and non-forest. The PDD model was then used to simulate pollen assemblages for different combinations of landscape arrangements (the Multiple Scenario Approach) that reflect possible anthropogenic and climate driven forest cover change in the late Holocene. We show that pollen records from large Amazonian lakes vary greatly in their sensitivity to forest loss depending on the baseline forest cover. Lakes in landscapes containing >80% forest will detect small reductions (5% of total cover), but this sensitivity degrades rapidly with forest cover loss. There are a wide range of uncertainties in pollen reconstructions from mosaic and ecotonal landscapes. In forest-savanna mosaics, large reductions of forest cover could be undetectable through the pollen record. In ecotonal landscapes, the relationship between forest cover and its representation in the pollen record rapidly weakens with increasing distance from the forest boundary. Further application of PDD modelling in combination with the Multiple Scenario Approach can address the uncertainties in pollen-based reconstructions of past land cover in the tropics, but require further investment and development.

**Keywords:** Amazonia, Forest clearance, Multiple Scenario Approach, Palaeoecology, Pollen Dispersal and Deposition Models, Pre-Columbian Impact

## Introduction

Pollen analysis is perhaps the most effective tool available to reconstruct past vegetation cover and it is applied globally. From vegetation reconstructions based on fossil pollen assemblages, researchers have determined historical biogeography and the climatic and human drivers of vegetation turnover in biomes from the tropics to the poles (e.g., Jackson et al., 1997; Brubaker et al., 2005; Gaillard et al., 2010; Flantua et al., 2016). Conventionally, pollen results are interpreted qualitatively and narratively, but in recent decades advances in modelling techniques have enabled palaeoecologists to derive spatially explicit reconstructions of land cover from relative abundances of different pollen types retrieved from peats and sediments (Gaillard et al., 2010; Trondman et al., 2015). In particular, Pollen Dispersal and Deposition (PDD) models, linking vegetation cover and pollen influx in lakes, have been instrumental in quantifying past land cover from European pollen records (Sugita, 2007; Gaillard et al., 2008b, 2008a; Trondman et al., 2015), including prehistoric human-modified landscapes (Brostrom et al., 2008; Gaillard et al., 2008a; Tipping et al., 2009). The enormous potential of these quantitative reconstruction methods have been harnessed by a wide group of users, such as the international working groups PAGES Landcover6k (Gaillard & LandCover6k Steering Group Members, 2015), which aims to develop historical land cover maps using these methods for the entire globe. Used in conjunction with the Multiple Scenario Approach (MSA) (Bunting & Middleton, 2009), where pollen deposition in a lake is simulated for a variety of synthetic landscapes that represent a range of possible configurations (Tipping et al., 2009), PDD models can provide powerful insights into how fossil pollen records might vary as a result of both changes in relative forest cover and patterning of vegetation mosaics of landscapes.

PDD reconstruction and simulation methods, however, are undeveloped in most tropical regions, where we also have fewest pollen records and consequently the biggest knowledge gaps around relative forest cover change due to human and climatic drivers. Pollen trap data have been derived for a variety of tropical ecosystems and these have greatly improved our understanding of pollen-plant relationships (Bonnefille et al., 1999; Gosling et al., 2005, 2009; Burn et al., 2010; Correa-Metrio et al., 2011; Julier et al., 2017). However, these studies rarely incorporate the spatially explicit plant distribution data that are required to calibrate the model for each vegetation type (e.g., Bunting et al., 2013), with a limited exception in Africa (Duffin & Bunting, 2008). Also, the PDD modelling approach differs in that it can be used to simulate pollen assemblages from vegetation communities, whereas pollen trap data studies use statistical methods to link empirical pollen data to the surrounding vegetation.

Many of the challenges facing palaeoecologists in applying PDD modelling to tropical regions are simply historical artefacts of limited calibration data. Palaeoecologists and vegetation mappers have been gathering datasets in northern temperate regions for nearly a century, whereas vast tropical regions lack this legacy of intensive research endeavour. These challenges, however, need to be met to address some of the most pressing questions in tropical biogeography. In Amazonia, in particular, discoveries of archaeological sites revealed because of recent deforestation (Mann, 2008; Pärssinen et al., 2009; Schaaf, 2012; de Souza et al. 2018) have raised the possibility that pre-Columbian people once cleared large tracts of rainforest to build these features, although this model of land clearance is disputed in recent studies (McMichael et al., 2014; Watling et al., 2017). Most of these insights into anthropogenic impacts on Amazonian forest have been gained through pollen analyses which have been narrative and qualitative in their interpretation (Bush et al., 2007, 2016; Urrego et al., 2013; Carson et al., 2014, 2015; Whitney et al., 2014; Brugger et al., 2016). Many of these sediment cores were extracted from large lakes (> 1 km radius), which are known in temperate regions to reflect a regional vegetation (ca.  $10^4$  -  $10^5$  km<sup>2</sup>) source, although this has not been confirmed for tropical ecosystems. The sensitivity of these records to forest clearance is uncertain, which has exacerbated the debate over the extent of pre-Columbian impact on Amazonian ecosystems (McMichael et al., 2012; Clement et al., 2015; Piperno et al., 2015).

Here, we employ PDD modelling combined with the MSA to simulate pollen assemblages for a variety of landscape arrangements to link forest pollen percentages to changing forest cover in Amazonian landscapes. The aims of this study are: (i) to determine the sensitivity of Amazonian pollen records from lake sediments to detecting change in forest cover; (ii) discuss the implications of the results for the interpretation of pollen records covering the archaeologically rich prehistoric period in Amazonia (ca. the last 2,000 years); and (iii) highlight the technical developments required to improve PDD modelling in tropical South America.

## Methods

### Geographical setting

Southwestern Amazonia is a geo-ecologically diverse region, the landscapes of which are characterized by sharply delimited forest-savanna mosaics (Fig. 1) (Pouilly & Beck, 2004; Langstroth, 2011), including the *Llanos de Moxos*, an Amazonian sub-basin defined by poorly drained compacted sediments. The *Llanos de Moxos* is seasonally flooded, therefore forest occupies local areas of higher micro-relief and well-drained soils such as the outcrops of the Precambrian Shield and river levees, and savanna occupies lower areas. This

geomorphology creates a diverse mosaic landscape with sharply defined forest-savanna boundaries (Pouilly & Beck, 2004; Langstroth, 2011).

The *Llanos de Moxos* and the wider southwestern Amazon region is immensely rich in archaeology, containing a diversity of Pre-Columbian earthwork structures (Erickson, 2006; Mann, 2008; Lombardo & Prümers, 2010; Schaan, 2012). Multiple palaeovegetation reconstructions in this region have been derived from sediment cores from large lakes (> 1 km) (e.g., Mayle et al., 2000; Whitney et al., 2013; Carson et al., 2014) from which human- and climatically-driven vegetation change have been inferred, but the sensitivity of these records to detecting changes in forest cover is uncertain. Reconstructing past anthropogenic forest clearance in this region is further complicated by a backdrop of increasing precipitation that began in the mid to late Holocene (Mayle et al., 2000; Baker et al., 2001; Flantua et al., 2016), which promoted the southward shift of the rainforest ecotone, the magnitude of which is unknown. Thus, disentangling what is climatic versus anthropogenically driven vegetation change is an unresolved question in the region (Maezumi et al., 2017). PDD modelling using synthetic landscapes that represent a variety of possible forest versus open ground scenarios can constrain the range of pollen signals that would be expected from human (e.g., Tipping et al., 2009) and climatically driven climate change.

## **Approach**

We calibrated a Pollen Dispersal and Deposition (PDD) model using a two-component (forest and non-forest) landscape in southwestern Amazonia, including the *Llanos de Moxos* (forest-savanna mosaic), and used this PDD model to constrain the range of uncertainty in pollen signals derived from large lakes. The Multiple Scenario Approach was employed to create synthetic landscapes to test the range of potential forest cover arrangements, reflecting both climate-driven ecotonal movement and past forest clearance. The following steps were undertaken to implement PDD modelling combined with the MSA in these landscapes:

1. Reconfiguration of the PDD model in R to enable the application of the Multiple Scenario Approach using a two-component landscape.
2. Selection of parameters suitable for Amazonian pollen and vegetation, based upon a review of existing literature on pollen-plant relationships.
3. Configuration of modern pollen and vegetation cover calibration datasets to fit a two-component landscape.
4. Determination of the 'Relative Pollen Productivity' for each landscape component (model calibration) using a Maximum Likelihood Approach.
5. Application of the calibrated PDD model to simulate pollen assemblages for lakes in a variety of synthetic landscapes arrangements.

## **Step 1. Model configuration and assumptions**

The model is well described elsewhere (Sugita, 1994; Bunting et al., 2004), but here we summarise briefly. Pollen loading ( $y_{ik}$ ) of plant group ( $i$ ) at a deposition site (or lake) ( $k$ ) is modelled as

$$y_{ik} = \sum \alpha_i \psi_{ik} \quad (\text{Equation 1})$$

where  $\psi_{ik}$  is the distance-weighted land cover of plant group  $i$  calculated using a taxon-specific weighting term incorporating parameters for atmospheric transport and for fall speed of pollen types and  $\alpha_i$  is the Relative Pollen Productivity of plant group  $i$  (Prentice, 1985; Sugita, 1994). PDD models simulate the pollen assemblage for a depositional environment, such as a lake surface or peat core, by summing the distance-weighted pollen production of pollen sources (i.e., the surrounding vegetation) in each landscape. We used the Sugita-Prentice model (Prentice, 1985; Sugita, 1993, 1994) which simulates pollen influx in lakes without substantial inflowing streams, and is a derivation of the widely-used Gaussian plume particle deposition model (Sutton, 1953; Prentice, 1985). It assumes neutral conditions for atmospheric mixing (Sugita, 2007) and assumes that most pollen is transported to the coring point by air flow above the plant canopy (Prentice, 1985), that the rate at which pollen grains settle out from the air is proportional to their sedimentation velocity (Prentice, 1985; Sugita, 1994), and that there is total mixing of pollen within the water body (Sugita, 1993), all of which can reasonably be assumed in our study systems. The PDD models, at present, assume a single release height for pollen, but they have been successfully applied to reconstructing openness of vegetation elsewhere (Nielsen, 2004). Pollen deposition was simulated for every pixel assigned to ‘water’ within the lake body and the results were summed (after Bunting & Middleton, 2005).

In many studies, the right hand term is divided into two components based on the distance of vegetation from the point where the pollen assemblage is forming, a local component from the basin edge to a defined distance, and a background component sourced from beyond that distance (Sugita, 1994, 2007). This was a computational necessity when work using this approach began, since the background component can be treated as a single constant term and therefore reduces the amount of calculations needed, but increases in available computing power allow us to simulate pollen loading from all relevant distances. We incorporated this regional background signal by using as large a landscape as was computationally feasible to ensure that the entire potential pollen source was included in the calibration. The maximum distance of 60 km from the lake centre encompasses the point at which the rate of change in pollen deposition approaches an asymptote (Fig. S1), beyond which changes in vegetation composition are not clearly registered in the pollen influx. Given that the ‘pollen source’ is an emergent property of the distance-weighting model chosen and the structure of the vegetation

mosaic modelled (Bunting et al., 2004), the use of large landscapes is a conservative approach because it does not assume a specific origin of the pollen.

## **Step 2. Model Parameters**

Parameters required for PDD models include pollen fall speeds and wind speed. Each component was represented in the simulated pollen loadings by a single taxon (forest = Moraceae; savanna/non-forest = Poaceae). Wind-pollinated Moraceae dominates rainforest communities in SW Amazonia (ter Steege et al., 2013), reflected in the abundance of the Moraceae/Urticaceae morphotype in pollen rain records (>60%) (Gosling et al., 2005). This morphotype was therefore used as an appropriate surrogate for Amazonian rainforest. The second component, non-forest or savanna, is represented by seasonally flooded savannas in the real landscape (Poaceae). The mean diameter of Moraceae/Urticaceae pollen as determined through morphological investigations of this pollen type (Burn & Mayle, 2008) was used to calculate a fall speed of 0.014 m/s using Stoke's Law (Gregory, 1973). This value approximates the reported fall speed for *Urtica* (Jackson & Lyford, 1999), a morphologically similar pollen grain of the same taxonomic order (Urticales). Similarly, given that grasses dominate the savanna herbaceous layer, we have chosen to use the fall speed estimated for grass to represent our non-forest component (Gaillard et al., 2008b) (0.035 m/s).

Different wind speeds were used for the calibration and experimental simulations. Wind speeds were extracted from the University of East Anglia's Climate Research Unit (CRU) dataset (New et al., 2000). The CRU dataset provides estimates of averaged wind speed between 1961 and 1990, which approximates the temporal resolution of the topmost 1-cm lake sediment analyzed for modern pollen. Most PDD modelling experiments use values of 3-4 m/s (Sugita et al., 1999; Bunting et al., 2004; Brostrom et al., 2008; Hellman et al., 2008). Model calibration was achieved using site (lake) specific modern wind speeds. For the simulation experiments, we used the mean Amazonian wind speed of 4.03 m/s and compared those findings to those using mean global wind speed (3.23 m/s). Given the wide range in pollen grain sizes, wind speed may have a marked effect on the findings.

## **Step 3. Calibration datasets**

Input pollen data were derived from surface pollen assemblages of nine published lake sites located in southwestern Amazonia (Table 1) with the pollen summed into 'forest' or 'non-forest' types. Total forest pollen spans a wide range of values in the calibration lake surface pollen assemblages (14 – 80%). A large proportion of all forest pollen types in the forest calibration signal (54 - 87%) belong to the order Urticales (Cannabaceae, Urticaceae, Moraceae, Ulmaceae). Therefore, the two-component landscape approach that necessitated a single pollen morphotype being assigned to forest pollen was appropriate for these ecosystem



types. The few additional forest pollen types that were recovered from the calibration datasets were predominantly *Alchornea*, *Gallesia* and *Acalypha*, which have a similar size to Urticales (Roubik & Moreno, 1991).

The mosaic landscape of SW Amazonia was classified into a two-component vegetation system (forest and non-forest). A similar highly simplified approach has been applied successfully to reconstruct past landscapes using PDDs in Denmark (Nielsen, 2004). This simplification of the landscape is appropriate for three reasons: (i) our questions concern relative cover of forest, not composition of different forest types; (ii) the most abundantly produced and well dispersed pollen types cannot be assigned to one forest type due to the ecological range of the contributing plant species, and the indicators of specific forest types occur in comparatively low abundance; and (iii) the two-class division captures the nature of the landscape in southwestern Amazonia in which the calibration sites are located when considered on a scale of  $\geq 1 \text{ km}^2$ , with its sharp community boundaries and clearly delineated savanna (non-forest) and forest mosaic. Regional vegetation data were derived from the Hansen et al. (2013) global forest cover dataset (a 30 m resolution tree canopy cover map for the year 2000). A 30 m resolution was prohibitively computationally expensive; therefore, we averaged all pixels to a 200 m grid. Finally, we classified all pixels containing water bodies as non-pollen producing pixels.

#### **Step 4. Model Calibration**

PDD models require a measure of pollen productivity of the source plant(s) or vegetation type relative to base value, the 'Relative Pollen Productivity' (RPP). A Maximum Likelihood approach was used to estimate the RPP of non-forest (savanna) relative to forest. Most empirical estimates of RPP are derived using the Extended R-value (ERV) approach (Parsons & Prentice, 1981; Prentice & Parsons, 1983), an iterative approach to parameter estimation developed for pollen-vegetation datasets with at least three taxa present. For our two-component system, a simpler approach could be used.

For the Maximum Likelihood calculations, we fixed forest RPP at 1 and varied the value for non-forest RPP. Potential pollen productivity values of non-forest relative to forest (hereafter  $\text{RPP}_{\text{f(s)}}$ ) were varied through a geometric series (0.125 to 16) and compared to the calibration datasets. RPPs have been shown to vary greatly through space and time (Brostrom et al., 2008; Duffin & Bunting, 2008; Mazier et al., 2012), even within a single study region. Therefore, providing a more precise measurement of RPP is unlikely to be ecologically meaningful (Andersen, 1970; Bunting et al., 2013). The pollen loadings for each lake pixel were then calculated for each potential  $\text{RPP}_{\text{f(s)}}$  value using the approach described above and averaged across the lake to get a well mixed estimate of pollen deposition. Wind speeds specific to each lake site were used (New et al., 2000). The source vegetation was weighted

by the Sutton-Prentice model relative to the depositional site (Sugita, 1994). This approach provides a simple but robust means of calibration when only two taxa are considered, and allows us to include pollen count uncertainties, as determined using Maher's method in Psimpoll 4.27 (Bennett, 2007) in the estimation of RPP. The likelihoods calculated for each calibration lake were summed for each potential  $RPP_f(s)$  value. The maximum likelihood was obtained where  $RPP_f(s) = 4$ ; therefore, this value was then used for the landscape simulations (Fig. S2).

### **Step 5. Simulation of Pollen Assemblages using MSA**

We created an ensemble of possible forest versus non-forest scenarios by generating clearances in synthetic landscapes that were designed to replicate potential landscape configurations in southwestern Amazonia. Forest pollen percentages were simulated in each synthetic landscape using the calibrated PDD model. To determine whether alterations in forest cover were detectable for a given scenario, changes in simulated forest pollen percentages needed to have exceeded the 95% confidence intervals on standard pollen counts from the calibration lakes in southwestern Amazonia ( $\pm 5\%$  Forest Pollen, calculated according to (Maher, 1972)). The simulation experiments are as follows: **Simulation I:** Two landscape parameters were varied: (i) the total proportion of forest and (ii) the size of the forest 'clearance' (e.g. patch size) relative to the lake (Fig. 2 a,b). **Simulation II:** Two landscape parameters were varied: (i) the total proportion of forest and (ii) the position of the lake relative to the forest boundary (Fig. 2 c,d).

The PDD model has been coded into R for this study (R v3.1.0, R Core Team, 2014). The R source code, GEORDIE-POLL (Generating Estimates Of Regional Deforestation In Ecosystems using POLLen), is available at <https://github.com/lsmallma/GeordiePol>.

## **Results**

### **Model parameters and uncertainties**

The Relative Pollen Productivity (RPP) of savanna was determined to be approximately four times that of forest. The high RPP of savanna is unexpected given that modern pollen rain studies from traps situated in nearby rainforest and savanna ecosystems (Gosling et al., 2009; Burn et al., 2010; Jones et al., 2011) have demonstrated that forest pollen, specifically Moraceae, is over-represented in Amazonian pollen assemblages as determined through pollen representation factors (ratio of percent abundance of pollen taxon to abundance of source plant relative to total individuals in the sample plot, after Davis (1963)). Pollen traps set within forest capture a large proportion of trunk space pollen (Jackson & Lyford, 1999), and will record gravity-deposited and insect-carried pollen, whilst the model used assumes only above-canopy pollen transport. In savanna, Moraceae stems are rare, but given that the vegetation canopy is open, and trap placement is above the herb layer, the trapped pollen will



contain less of the local component but more pollen transported originating from the closest forest canopies where Moraceae is abundant. Large lakes without substantial inflowing rivers are expected to receive pollen almost entirely from the above-canopy air transport route, and therefore do not behave like either of the trap situations considered. Pollen signatures differ depending on vegetation structure and depositional environment (e.g. Bunting 2008), and given that our research questions are concerned with the representation of forest pollen in large lakes, parameterising and using a model of above-canopy transport is the most appropriate option for our modelling approach.

The influence of wind speed on Pollen Dispersal and Deposition (PDD) model outputs is shown in Fig. 3, where there is a significant difference in modelled pollen loading using mean Amazonian (4.03 m/s) and global (3.23 m/s) wind speeds for most clearance scenarios. The sensitivity of PDD modelling to this parameter, which is compounded by the broad range in grain size of Amazonian pollen, shows that wind speed can provide a considerable source of uncertainty in PDD modelling. Wind speed is difficult to estimate, especially in palaeoenvironmental contexts when climate systems were different to modern, but the trend is broadly similar for different wind speeds, showing that percent forest pollen is most under-represented for mid-range forest cover, thus overall trends are useful for understanding the relationship between varying landscape composition and the pollen signal. The results presented here provide minimum estimates of the uncertainties resulting from the ability of fossil pollen records to detect forest cover change; the true range of uncertainty is likely higher than that which is captured by these simulations (Fig. 3).

### **Experimental results**

Simulation Experiment I (Fig. 3) shows that small changes in forest cover (ca. 5%) are more sensitively registered in a densely forested landscape (> 80% forest cover) than a partially forest covered one, thus large lakes (> 1 km diameter) in closed-canopy rainforest can detect low levels (> 5%) of forest clearance. The sensitivity to a small change degrades rapidly as overall forest cover levels decrease, resulting in a narrower range of simulated pollen assemblages, indicating that landscape patterning (spatial arrangement of forest versus non-forest) at the scales modelled is not detected by large lakes in the model outputs in mosaic landscapes or partially cleared landscapes.

Strikingly, almost half the arboreal cover in mosaic forest-savanna landscapes can be removed without influencing the pollen signal beyond the pollen count error. The highest variability in percent forest pollen among simulated pollen assemblages occurs for larger patch sizes ( $r = 2400$  m) in landscape scenarios with mid-range forest cover (i.e., mosaic), yet percent forest pollen variability (ca. 8%) in these simulations is less than the count error of

the fossil pollen data ( $\pm 5\%$ ) (Maher, 1972) from large lake sites, thus the signal-to-noise ratio of the fossil pollen data is too low to detect these landscape changes.

In the ecotone movement Simulation Experiment II (Fig. 4), the relationship between percent forest cover and percent forest pollen rapidly weakens with increasing distance of the lake from the forest boundary. For example, to achieve a 10% drop in forest pollen, a 30% reduction of closed-canopy rainforest is required when the lake is located at the boundary, but 40% when the lake is 5 km away from the forest boundary. More importantly, however, simulation experiment II shows that various combinations of ecologically-distinct landscape arrangements can produce identical percentages of forest pollen, which highlights the problem of equifinality in the application of landscape reconstruction algorithms (e.g. Sugita, 2007; Bunting & Middleton, 2009). For example, 5% clearance of closed-canopy rainforest where the lake is positioned at the forest boundary produces the same pollen signal as 40% clearance where the lake is located 20 km distant.

## Discussion

The lack of quantitative pollen-based reconstructions of past vegetation cover has served to fuel the debate over the extent of Pre-Columbian impact in the Amazon (Clement et al., 2015; Piperno et al., 2015). Our simulation experiments show that pollen records from large lakes ( $> 1$  km diameter) in closed-canopy rainforest are more sensitive to detecting forest clearance than similar sized lakes in forest-savannah mosaics. For these rainforest lakes, where there is palaeoecological evidence of crop cultivation (maize, manioc) and/or charcoal but no significant decline in percent forest pollen, forest clearance in the catchment will most likely have been minimal ( $< 5\%$ ), probably reflecting agroforestry practices and crop cultivation that maintains canopy structure (Clement et al., 2015), such as is demonstrated by Maezumi et al., (2017). We demonstrate that, although pollen records from these large rainforest lakes are, by and large, insensitive to detecting patterning (i.e., size of forest clearings) within the landscape, they are sensitive to detecting small changes ( $> 5\%$ ) in the overall proportion of forest vs non-forest, as long as the baseline catchment was predominantly forested. At present, the PDD modelling reflects the relative proportion of forest cover only; its use to determine potential human impact on forest composition, such as promotion of economically useful taxa, requires further calibration data and model development.

The modelled outputs are corroborated by studies based on palaeobotanical and charcoal data that demonstrate human impact on relative forest cover was low in interfluvial regions of western Amazonia (McMichael et al., 2012; Watling et al., 2017). Even where large Amazonian lake records have registered a substantial reduction in forest pollen (ca. 30%) associated with maize cultivation, such as at Lake Sauce in lowland Peru (Bush et al., 2016), the corresponding change in relative forest cover as determined through PDD modelling is

much lower (10 – 15%) than the pollen percentages alone would suggest. Our simulations, therefore, demonstrate that not only do palaeoecological records in western Amazonia point towards low impact on forest cover in prehistoric times (Bush et al., 2007, 2016; Urrego et al., 2013), pollen-based reconstructions in dense rainforest also provide the lowest uncertainty.

By contrast, the simulations show that pollen records situated in mosaic and ecotonal regions can represent a broad range of scenarios in terms of relative cover of forest versus non-forest with similar percent forest pollen values. Given this high uncertainty associated with pollen records in these mosaic landscapes, we can only describe *potential* forest clearance, but equally, the forest could have been left intact, as argued for the Monumental Mound Region of the *Llanos de Moxos* by Whitney et al., (2013). Whilst our discussion of human impact in mosaic and ecotonal areas gives the impression of minor ‘edge effects’ on Amazonian rainforest, these regions represent a large portion of land surface. The forest-savanna mosaics of the *Llanos de Moxos*, Pantanal, and Gran Sabana cover a combined 400,000 km<sup>2</sup>, and are known major regions of past human habitation and landscape modification.

Additionally, palaeoecological and palaeoclimatological evidence shows the extent of mosaic regions was likely far greater in the mid Holocene, as lower and more seasonal rainfall restricted the extent of rainforest in the southern margin of the Amazon catchment (Mayle et al., 2000; Baker et al., 2001; Carson et al., 2014) and may have promoted a greater extent of forest-savanna mosaic. The seasonal environments of southern Amazon coincide with archaeological evidence of large, complex prehistoric societies across the region (de Souza et al., 2018), and it is here that drier conditions during the mid Holocene are likely to have resulted in wider expanses of savanna and mosaic vegetation compared to modern (Mayle & Power, 2008). Our modelling results imply that as precipitation increased in southern Amazonia in the late Holocene, the sensitivity of pollen records to clearances would have increased as rainforest became established. Future investigations of human impacts on forest cover must consider how the sensitivity of lake pollen records varies with climatically-driven shifts in regional vegetation. The spatial extent of the changing position of the rainforest ecotone in the late Holocene, however, is poorly defined and considerably more palaeoenvironmental research is required to define both the natural and anthropogenic forcings of vegetation change in this vast region. PDD modelling can help to disentangle the climatic and anthropogenic influences on land cover, but a higher density of local-scale (ca. 100 m radius) lake sites to pinpoint ecotone position and speed of movement is also required.

The Sugita-Prentice model applied here reflects changes in the relative proportion of forest cover in a regional landscape. Alternative PDD models, such as Lagrangian Stochastic modelling, may have greater accuracy than the Sugita-Prentice model on regional scales

(Kuparinen et al., 2007; Theuerkauf et al., 2016), but requires specification of a greater number of atmospheric parameters which are likely to add more uncertainty in the outputs, especially for the South American tropics. Although this study describes a positive step forward in applying PDD modelling to tropical landscapes, greater efforts of collaboration, model development and modern vegetation-pollen data collection will be required to bring PDD modelling to lesser studied regions of the globe, such as Amazonia, to address some of the biggest questions in historical biogeography.

## Conclusions

We have made many assumptions in our experimental design, such as simplifying the landscape to forest versus non-forest and creating all-or-nothing clearances in forest. Despite these simplifications, Pollen Dispersal and Deposition (PDD) modelling and the Multiple Scenario Approach (MSA) have shown they are potentially enormously powerful tools that can be used to identify and mitigate the uncertainties in pollen-based reconstructions and to make the best use of the records from cores from remote regions where their retrieval is time-consuming and expensive. The MSA allows for the use of *a priori* landscape information generated through other proxy investigations to provide further constraints on the number of possible landscape scenarios (e.g., Tipping et al., 2009). Analysts can make use of environmental (e.g., soil fertility, water access, topography) and archaeological data (e.g., agricultural practice, population density) to constrain the range of possible landscape scenarios. The use of PDD modelling in advance of fieldwork allows palaeoecologists to test the sensitivity of target lake sites to hypothesized land cover change with the aim of assessing whether a record from the site can address the research questions of interest, thereby increasing the effectiveness of resource allocation. PDD modelling in Amazonia and other tropical regions, however, is a nascent field and requires investment and further collaboration in collecting calibration data, testing model outputs and further development for the particular characteristics of tropical ecosystems and landscapes. The combination of empirical pollen data, geographical information, and the Multiple Scenario Approach, shown here, can provide a very powerful tool to support collaboration between archaeologists and palaeoecologists for quantifying past human impact on rainforest across the little explored expanses of Amazonia.

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### Author contributions

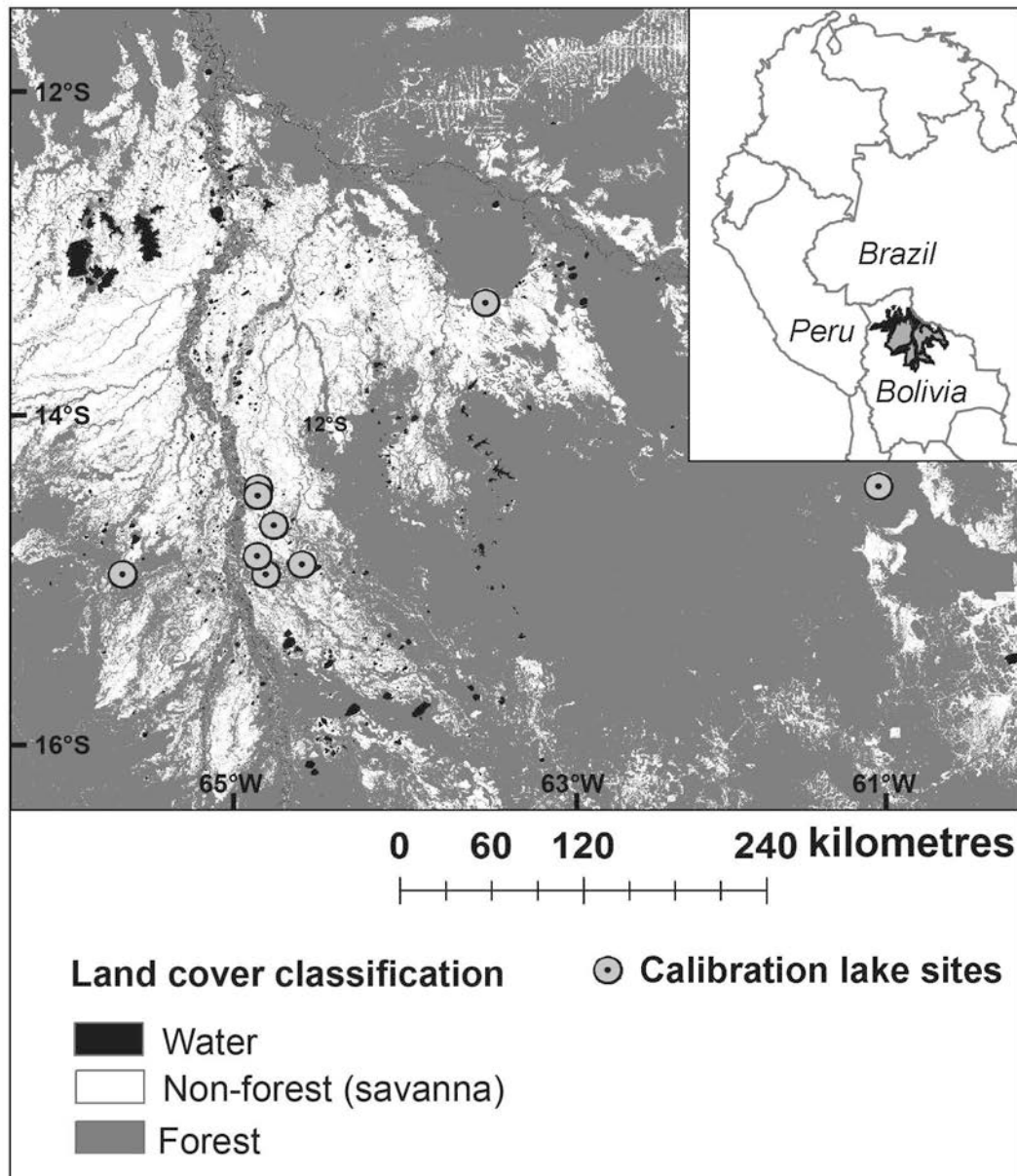
BSW conceived and developed the research project and led the writing of the manuscript; TLS coded the model, co-designed and ran the experiments; ETAM prepared the remote sensing data; JFC, FEM commented on the palaeoecological and archaeological context of the research; and MJB was instrumental in developing the conceptual framework for the modelling approach. All authors contributed to the interpretation and discussion of the results and the writing of the manuscript.

**Table 1.** Locations and parameters of lakes used for calibrating the PDD model

Lake	Latitude (S)	Longitude (W)	Area (km <sup>2</sup> )	Forest (%AP)	lower 95%	upper 95%	Publication
Laguna Azul	14°59'27"	64°48'45"	1.4	14.2	10.7	18.6	Jones et al., 2011
Laguna Belen	14°27'28"	64°51'30"	3.4	14.2	10.7	18.6	Jones et al., 2011
Laguna Suarez	14°52'51"	64°51'59"	6.7	23.1	18.7	28.2	Jones et al., 2011
Laguna Cernandez	14°41'18"	64°45'55"	15.5	26.8	22.1	32.1	Jones et al., 2011
Laguna Coitarama	14°30'10"	64°51'39"	5.8	25.1	20.5	30.3	Jones et al., 2011
Laguna Isireri	14°59'27"	65°40'21"	18.9	71	65.6	75.8	Burn et al., 2010
Laguna San Jose	14°56'28"	64°28'37"	16.0	28	23.2	33.3	Whitney et al., 2013
Laguna Oricore	13°20'46"	63°31'30"	11.5	67	61.5	72.1	Carson et al., 2014
Laguna Chaplin	14°28'30"	61°03'42"	8.1	80	75.1	84.1	Mayle et al., 2000; Burbridge et al., 2004

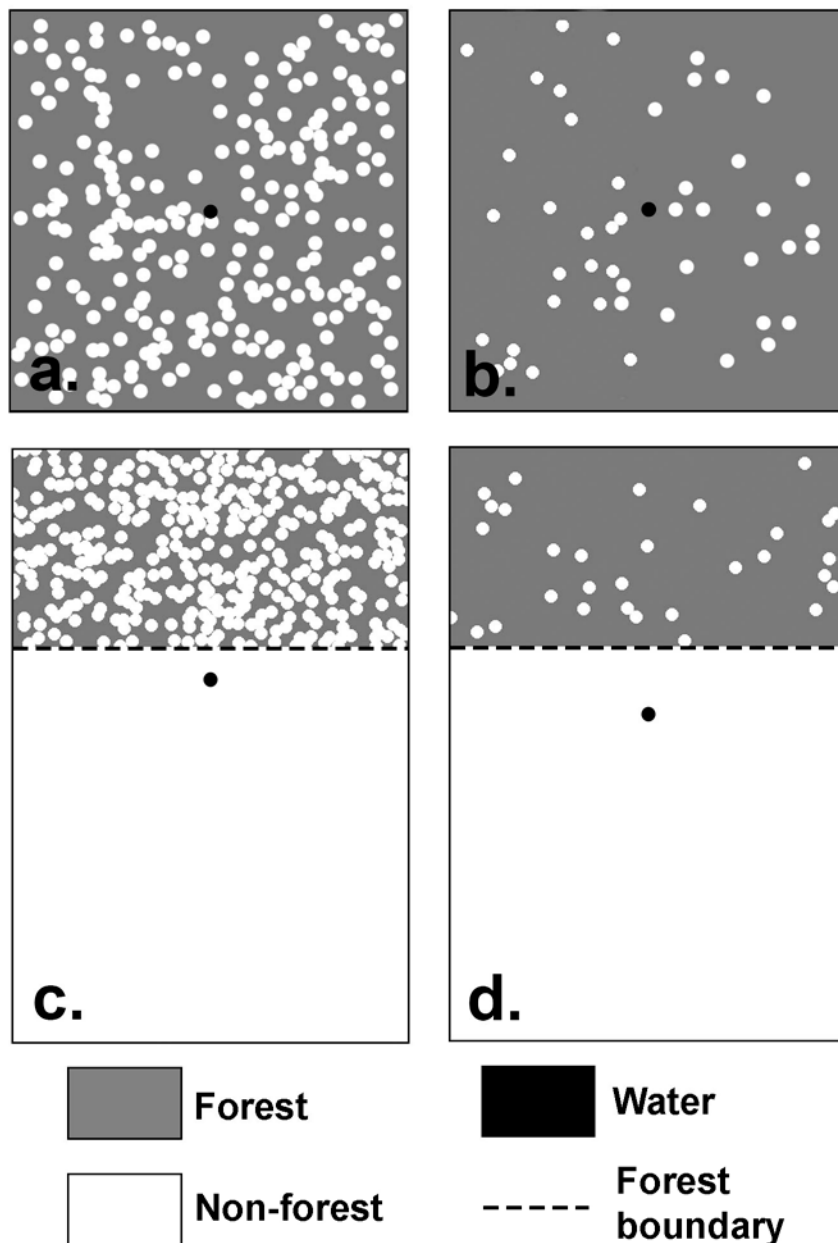
### Figures



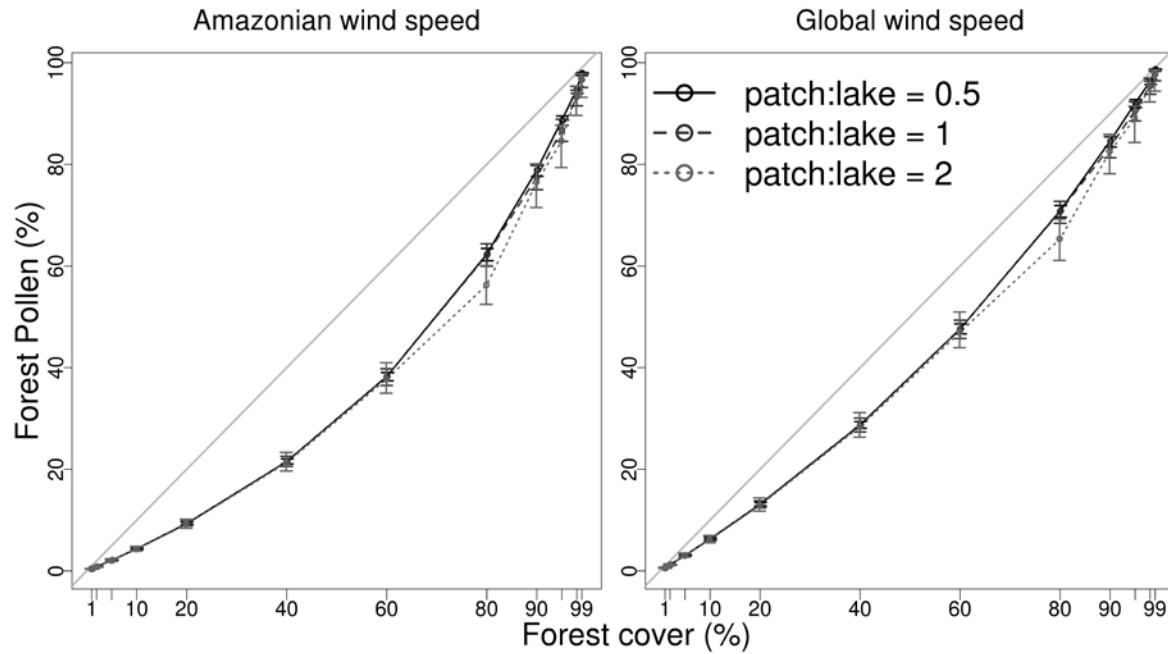


**Figure 1:** (a) Regional map of southwestern Amazonia, showing the southern limit of the Amazonian rainforest and the savanna-forest mosaic of the *Llanos de Moxos*. Forest cover dataset was derived from Hansen et al., (2013). Pixels were aggregated to 200m resolution and assigned to the forest category where they exceeded 30% cover, as is standard forest definition (Sexton et al., 2016).

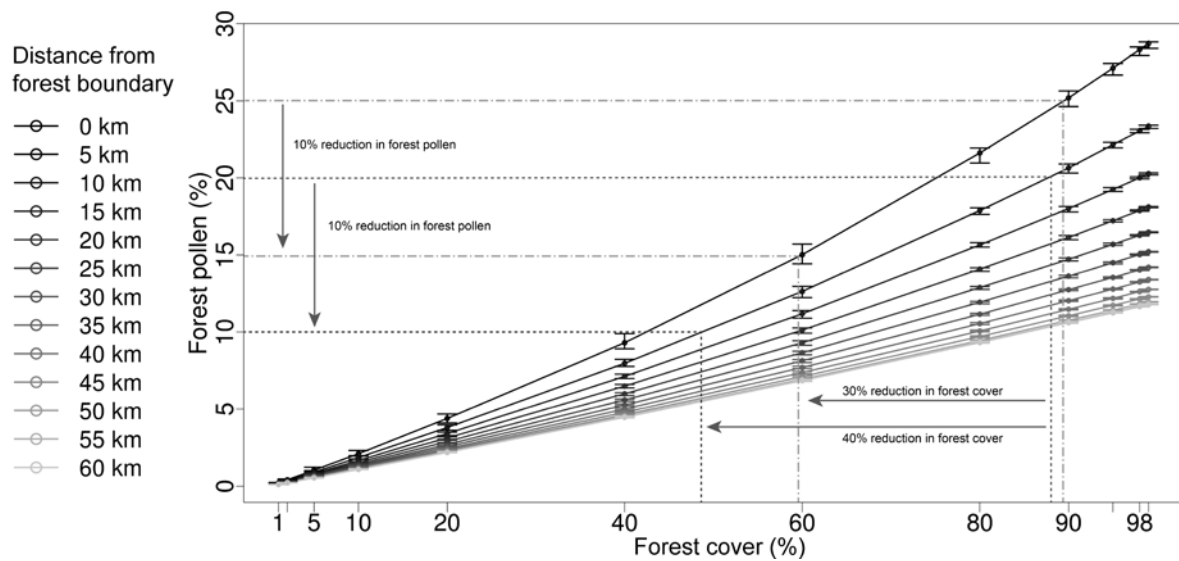




**Figure 2:** Examples of synthetic landscapes used for PDD modelling. For Simulation Experiment I, the proportion of forest cleared was varied for each landscape scenario. Example synthetic landscapes shown: **(a)** 20% landscape clearance and **(b)** 5% landscape clearance. For Simulation Experiment II, the position of the forest boundary relative to the lake was moved in 5 km increments, and for each ecotone position, proportion of forest cleared was also varied. **(c)** 50% clearance at 5 km and **(d)** 5% clearance at 10 km distance from forest boundary. In all simulations, clearances were made within forest in a two-component landscape and pollen loading was simulated in a round large lake ( $r = 1200$  m) positioned at the centre of each landscape.



**Figure 3:** Results of Simulation Experiment I for mean Amazonian (4.03 m/s) and Global (3.23 m/s) wind speeds. Clearance patches were randomly generated and repeated 1000 times to estimate uncertainty. Clearance patch size areas were varied relative to the lake surface area; (black) half lake size; (grey) equal to lake size; (light grey) twice lake size.



**Figure 4:** Results of Simulation Experiment II. Lake position relative to the ecotone was varied for each series. Line shading reflects distance from the forest boundary where the black line represents lake position at the ecotone boundary and lighter shades show simulations results with increasing distance from the forest boundary in 5 km increments. Dashed lines highlight the example discussed in the text, where equal reductions in forest pollen (10%) at the forest boundary (0 km) and 5 km distant reflect 30% and 40% reductions in forest cover, respectively. Simulations were performed with mean Amazonian wind speed (4.03 m/s) and clearance patch sizes were equal to the lake area.

## References

- Andersen, S.T. (1970) The relative pollen productivity and pollen representation of North European trees, and correction factors for tree pollen spectra. Determined by surface pollen analyses from forests. C.A. Reitzel, Copenhagen.
- Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D., & Broda, J.P. (2001) The history of South American tropical precipitation for the past 25,000 years. *Science*, **291**, 640-643.
- Bennett, K.D. (2007) Manual for psimpoll and pscomb. Available at [http://www.chrono.qub.ac.uk/psimpoll/psimpoll\\_manual/4.26/psman5.htm](http://www.chrono.qub.ac.uk/psimpoll/psimpoll_manual/4.26/psman5.htm) (accessed 12-04-2018)
- Bonnefille, R., Anupama, K., Barboni, D., Pascal, J., Prasad, S., & Sutra, J.P. (1999) Modern pollen spectra from tropical South India and Sri Lanka: altitudinal distribution. *Journal of Biogeography*, **26**, 1255–1280.
- Brostrom, A., Nielsen, A.B., Gaillard, M.-J., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A., Rasanen, S., Soepboer, W., von Stedingk, H., Suutari, H., & Sugita, S. (2008) Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. *Vegetation History and Archaeobotany*, **17**, 461–478.
- Brubaker Linda B., Anderson Patricia M., Edwards Mary E., & Lozhkin Anatoly V. (2005) Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of Biogeography*, **32**, 833–848.
- Brugger, S.O., Gobet, E., van Leeuwen, J.F.N., Ledru, M.-P., Colombaroli, D., van der Knaap, W.O., Lombardo, U., Escobar-Torrez, K., Finsinger, W., Rodrigues, L., Giesche, A., Zarate, M., Veit, H., & Tinner, W. (2016) Long-term man–environment interactions in the Bolivian Amazon: 8000 years of vegetation dynamics. *Quaternary Science Reviews*, **132**, 114–128.
- Bunting, M.J. (2008) Pollen in wetlands: using simulations of pollen dispersal and deposition to better interpret the pollen signal. *Biodiversity and conservation*, **17**, 2079-2096.
- Bunting, M.J., Farrell, M., Broström, A., Hjelle, K.L., Mazier, F., Middleton, R., Nielsen, A.B., Rushton, E., Shaw, H., & Twiddle, C.L. (2013) Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of Quaternary land cover. *Quaternary Science Reviews*, **82**, 41–55.
- Bunting, M.J., Gaillard, M.-J., Sugita, S., Middleton, R., & Broström, A. (2004) Vegetation structure and pollen source area. *The Holocene*, **14**, 651–660.
- Bunting, M.J. & Middleton, D. (2005) Modelling pollen dispersal and deposition using HUMPOL software, including simulating windroses and irregular lakes. *Review of Palaeobotany and Palynology*, **134**, 185–196.

- Bunting, M.J. & Middleton, R. (2009) Equifinality and uncertainty in the interpretation of pollen data: the Multiple Scenario Approach to reconstruction of past vegetation mosaics. *Holocene*, **19**, 799–803.
- Burn, M.J. & Mayle, F.E. (2008) Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology. *Review of Palaeobotany and Palynology*, **149**, 187–201.
- Burn, M.J., Mayle, F.E., & Killeen, T.J. (2010) Pollen-based differentiation of Amazonian rainforest communities and implications for lowland palaeoecology in tropical South America. *Palaeogeography Palaeoclimatology Palaeoecology*, **295**, 1–18.
- Bush, M.B., Correa-Metrio, A., McMichael, C.H., Sully, S., Shadik, C.R., Valencia, B.G., Guilderson, T., Steinitz-Kannan, M., & Overpeck, J.T. (2016) A 6900-year history of landscape modification by humans in lowland Amazonia. *Quaternary Science Reviews*, **141**, 52–64.
- Bush, M.B., Silman, M.R., de Toledo, M.B., Listopad, C., Gosling, W.D., Williams, C., de Oliveira, P.E., & Krisel, C. (2007) Holocene fire and occupation in Amazonia: records from two lake districts. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **362**, 209–218.
- Carson, J.F., Watling, J., Mayle, F.E., Whitney, B.S., Iriarte, J., Prümers, H., & Soto, J.D. (2015) Pre-Columbian land use in the ring-ditch region of the Bolivian Amazon. *The Holocene*, **25**, 1285–1300.
- Carson, J.F., Whitney, B.S., Mayle, F.E., Iriarte, J., Pruemers, H., Soto, J.D., & Watling, J. (2014) Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 10497–10502.
- Clement, C.R., Denevan, W.M., Heckenberger, M.J., Junqueira, A.B., Neves, E.G., Teixeira, W.G., & Woods, W.I. (2015) The domestication of Amazonia before European conquest. *Proceedings of the Royal Society B*, **282**, 20150813.
- Correa-Metrio, A., Bush, M.B., Pérez, L., Schwalb, A., & Cabrera, K.R. (2011) Pollen distribution along climatic and biogeographic gradients in northern Central America. *The Holocene*, **21**, 681–692.
- Davis, M.B. (1963) On the theory of pollen analysis. *American Journal of Science*, **261**, 897–912.
- Duffin, K.I. & Bunting, M.J. (2008) Relative pollen productivity and fall speed estimates for southern African savanna taxa. *Vegetation History and Archaeobotany*, **17**, 507–525.
- Erickson, C.L. (2006) The domesticated landscapes of the Bolivian Amazon. *Time and Complexity in Historical Ecology: Studies in the Neotropical Lowlands* (ed. by W. Balee and C.L. Erickson), pp. 235–278.
- Flantua, S., Hooghiemstra, H., Vuille, M., Behling, H., Carson, J., Gosling, W., Hoyos, I., Ledru, M., Montoya, E., Mayle, F., & others (2016) Climate variability and human

- impact in South America during the last 2000 years: synthesis and perspectives from pollen records. *Climate of the Past*, **12**, 483–523.
- Gaillard, M.-J. & LandCover6k Steering Group Members (2015) LandCover6k: Global anthropogenic land-cover change and its role in past climate. **23**, 38–39.
- Gaillard, M.-J., Sugita, S., Bunting, J., Dearing, J., & Bittmann, F. (2008a) Human impact on terrestrial ecosystems, pollen calibration and quantitative reconstruction of past land-cover. *Vegetation History and Archaeobotany*, **17**, 415–418.
- Gaillard, M.-J., Sugita, S., Bunting, M.J., Middleton, R., Brostrom, A., Caseldine, C., Giesecke, T., Hellman, S.E.V., Hicks, S., Hjelle, K., Langdon, C., Nielsen, A.-B., Poska, A., von Stedingk, H., Veski, S., & Members, P. (2008b) The use of modelling and simulation approach in reconstructing past landscapes from fossil pollen data: a review and results from the POLLANDCAL network. *Vegetation History and Archaeobotany*, **17**, 419–443.
- Gaillard, M.-J., Sugita, S., Mazier, F., et al. (2010) Holocene land-cover reconstructions for studies on land cover-climate feedbacks. *Climate of the Past*, **6**, 483–499.
- Gosling, W.D., Mayle, F.E., Tate, N.J., & Killeen, T.J. (2005) Modern pollen-rain characteristics of tall terra firme moist evergreen forest, southern Amazonia. *Quaternary Research*, **64**, 284–297.
- Gosling, W.D., Mayle, F.E., Tate, N.J., & Killeen, T.J. (2009) Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Review of Palaeobotany and Palynology*, **153**, 70–85.
- Gregory, P.H. (1973) *The microbiology of the atmosphere*. Wiley, New York.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., & Townshend, J.R.G. (2013) High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, **342**, 850–853.
- Hellman, S., Gaillard, M.-J., Broström, A., & Sugita, S. (2008) The REVEALS model, a new tool to estimate past regional plant abundance from pollen data in large lakes: validation in southern Sweden. *Journal of Quaternary Science*, **23**, 21–42.
- Jackson, S.T. & Lyford, M.E. (1999) Pollen dispersal models in Quaternary plant ecology: Assumptions, parameters, and prescriptions. *The Botanical Review*, **65**, 39–75.
- Jackson, S.T., Overpeck, J.T., Webb, T., Keatts, S.E., & Anderson, K.H. (1997) Mapped plant-macrofossil and pollen records of late quaternary vegetation change in Eastern North America. *Quaternary Science Reviews*, **16**, 1–70.
- Jones, H.T., Mayle, F.E., Pennington, R.T., & Killeen, T.J. (2011) Characterisation of Bolivian savanna ecosystems by their modern pollen rain and implications for fossil pollen records. *Review of Palaeobotany and Palynology*, **164**, 223–237.

- Julier, A.C., Jardine, P.E., Adu-Bredu, S., Coe, A.L., Duah-Gyamfi, A., Fraser, W.T., Lomax, B.H., Malhi, Y., Moore, S., Owusu-Afriyie, K., & others (2017) The modern pollen–vegetation relationships of a tropical forest–savannah mosaic landscape, Ghana, West Africa. *Palynology*, 1–15.
- Kuparinen, A., Markkanen, T., Riikonen, H., & Vesala, T. (2007) Modeling air-mediated dispersal of spores, pollen and seeds in forested areas. *Ecological Modelling*, **208**, 177–188.
- Langstroth, R. (2011) Biogeography of the Llanos de Moxos: natural and anthropogenic determinants. *Geographica Helvetica*, **3**, 183–192.
- Lombardo, U. & Prümers, H. (2010) Pre-Columbian human occupation patterns in the eastern plains of the Llanos de Moxos, Bolivian Amazonia. *Journal of Archaeological Science*, **37**, 1875–1885.
- Maezumi, S.Y., Whitney, B.S., Mayle, F.E., Gregorio de Souza, J., & Iriarte, J. (2017) Reassessing climate and pre-Columbian drivers of paleofire activity in the Bolivian Amazon. *Quaternary International*, DOI: 10.1016/j.quaint.2017.11.053
- Maher, L.J. (1972) Nomograms for computing 0.95 confidence limits of pollen data. *Review of Palaeobotany and Palynology*, **13**, 85–93.
- Mann, C.C. (2008) Ancient Earthmovers of the Amazon. *Science*, **321**, 1148–1152.
- Mayle, F.E., Burbridge, R., & Killeen, T.J. (2000) Millennial-scale dynamics of southern Amazonian rain forests. *Science*, **290**, 2291–2294.
- Mayle, F.E. & Power, M.J. (2008) Impact of a drier Early–Mid-Holocene climate upon Amazonian forests. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **363**, 1829–1838.
- Mazier, F., Nielsen, A.B., Broström, A., Sugita, S., & Hicks, S. (2012) Signals of tree volume and temperature in a high-resolution record of pollen accumulation rates in northern Finland. *Journal of Quaternary Science*, **27**, 564–574.
- McMichael, C.H., Palace, M.W., & Golightly, M. (2014) Bamboo-dominated forests and pre-Columbian earthwork formations in south-western Amazonia. *Journal of Biogeography*, **41**, 1733–1745.
- McMichael, C.H., Piperno, D.R., Bush, M.B., Silman, M.R., Zimmerman, A.R., Raczka, M.F., & Lobato, L.C. (2012) Sparse Pre-Columbian Human Habitation in Western Amazonia. *Science*, **336**, 1429–1431.
- New, M., Hulme, M., & Jones, P. (2000) Representing twentieth-century space-time climate variability. Part II: Development of 1901–96 monthly grids of terrestrial surface climate. *Journal of Climate*, **13**, 2217–2238.
- Nielsen, A.B. (2004) Modelling pollen sedimentation in Danish lakes at c.ad 1800: an attempt to validate the POLLSCAPE model. *Journal of Biogeography*, **31**, 1693–1709.



- Parsons, R. & Prentice, I. (1981) Statistical approaches to R-values and the pollen—vegetation relationship. *Review of Palaeobotany and Palynology*, **32**, 127–152.
- Pärssinen, M., Schaaf, D., & Ranzi, A. (2009) Pre-Columbian geometric earthworks in the upper Purús: A complex society in western Amazonia. *Antiquity*, **83**, 1084–1095.
- Piperno, D.R., McMichael, C., & Bush, M.B. (2015) Amazonia and the Anthropocene: What was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? *The Holocene*, **25**, 1588–1597.
- Pouilly, M. & Beck, S.G. (2004) Geografía general. Diversidad Biológica en la Llanura de Inundación del Río Mamoré: Importancia Ecológica de la Dinámica fluvial (ed. by M. Pouilly, S.G. Beck, M. Moraes, and C. Ibañez), pp. 15–26. Centro de Ecología Simón I. Patiño, Santa Cruz, Bolivia.
- Prentice, I. & Parsons, R. (1983) Maximum likelihood linear calibration of pollen spectra in terms of forest composition. *Biometrics*, 1051–1057.
- Prentice, I.C. (1985) Pollen representation, source area, and basin size: Toward a unified theory of pollen analysis. *Quaternary Research*, **23**, 76–86.
- Roubik, D.W. & Moreno, J.E.P. (1991) Pollen and spores of Barro Colorado Island. Missouri Botanical Garden, St. Louis, USA
- Schaaf, D.P. (2012) Sacred Geographies of Ancient Amazonia: Historical Ecology of Social Complexity. Left Coast Press, Walnut Creek.
- Sexton, J.O., Noojipady, P., Song, X.-P., Feng, M., Song, D.-X., Kim, D.-H., Anand, A., Huang, C., Channan, S., Pimm, S.L., & Townshend, J.R. (2016) Conservation policy and the measurement of forests. *Nature Climate Change*, **6**, 192–196.
- Souza, J.G., Schaaf, D.P., Robinson, M., Barbosa, A.D., Aragão, L.E.O.C., Jr, B.H.M., Marimon, B.S., Silva, I.B., Khan, S.S., Nakahara, F.R., & Iriarte, J. (2018) Pre-Columbian earth-builders settled along the entire southern rim of the Amazon. *Nature Communications*, **9**, 1125.
- ter Steege, H. ter, Pitman, N.C.A., Sabatier, D., et al. (2013) Hyperdominance in the Amazonian Tree Flora. *Science*, **342**, 1243092.
- Sugita, S. (1993) A Model of Pollen Source Area for an Entire Lake Surface. *Quaternary Research*, **39**, 239–244.
- Sugita, S. (1994) Pollen Representation of Vegetation in Quaternary Sediments: Theory and Method in Patchy Vegetation. *Journal of Ecology*, **82**, 881–897.
- Sugita, S. (2007) Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. *Holocene*, **17**, 229–241.
- Sugita, S., Gaillard, M.-J., & Broström, A. (1999) Landscape openness and pollen records: a simulation approach. *The Holocene*, **9**, 409–421.
- Sutton, O.G. (1953) *Micrometeorology*. McGraw-Hill, New York, USA.

- Theuerkauf, M., Couwenberg, J., Kuperinen, A., & Liebscher, V. (2016) A matter of dispersal: REVEALSinR introduces state-of-the-art dispersal models to quantitative vegetation reconstruction. *Vegetation History and Archaeobotany*, **25**, 541–553.
- Tipping, R., Bunting, M.J., Davies, A.L., Murray, H., Fraser, S., & McCulloch, R. (2009) Modelling land use around an early Neolithic timber “hall” in north east Scotland from high spatial resolution pollen analyses. *Journal of Archaeological Science*, **36**, 140–149.
- Trondman, A.-K., Gaillard, M.-J., Mazier, F., et al. (2015) Pollen-based quantitative reconstructions of Holocene regional vegetation cover (plant-functional types and land-cover types) in Europe suitable for climate modelling. *Global Change Biology*, **21**, 676–697.
- Urrego, D.H., Bush, M.B., Silman, M.R., Niccum, B.A., De La Rosa, P., McMichael, C.H., Hagen, S., & Palace, M. (2013) Holocene fires, forest stability and human occupation in south-western Amazonia. *Journal of Biogeography*, **40**, 521–533.
- Watling, J., Iriarte, J., Mayle, F.E., Schaaf, D., Pessenda, L.C., Loader, N.J., Street-Perrott, F.A., Dickau, R.E., Damasceno, A., & Ranzi, A. (2017) Impact of pre-Columbian “geoglyph” builders on Amazonian forests. *Proceedings of the National Academy of Sciences*, 201614359.
- Whitney, B.S., Dickau, R., Mayle, F.E., Soto, J.D., & Iriarte, J. (2013) Pre-Columbian landscape impact and agriculture in the Monumental Mound region of the Llanos de Moxos, lowland Bolivia. *Quaternary Research*, **80**, 207–217.
- Whitney, B.S., Dickau, R., Mayle, F.E., Walker, J.H., Daniel Soto, J., & Iriarte, J. (2014) Pre-Columbian raised-field agriculture and land use in the Bolivian Amazon. *The Holocene*, **24**, 231–241.